Forum

A reappreciation of 'conformity'

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Whiten & van de Waal (this volume) present an answer to a critical account of their conformity interpretations (van Leeuwen et al., 2015). Their target study (van de Waal et al., 2013) evidenced immigrant male vervet monkeys adjusting their food colour preferences to the preference demonstrated by the resident vervets, which was interpreted in terms of conformity. Van Leeuwen and colleagues (2015; also see van Leeuwen & Haun, 2013 and online commentary by Tennie, Fischer, Galef & Haun, 2013, at Sciencemag.org) acknowledged the insight gained from the reported observations for our understanding of social learning processes in wild primates, but criticized van de Waal et al.'s conformity interpretation (2013) as alternative learning

biases, other than conformity, could not be ruled out. In their reply to this critique, Whiten & van de Waal (this volume) systematically list their arguments against alternative explanations. Whiten & van de Waal (this volume) also present new data indicating that in their target study (2013) the "majority of individuals" opting to perform a specific behaviour correlated with the "majority of behaviours" performed across the population, thereby adding to a recent debate about how "the majority" should be operationalized in order to study conformist transmission (see Aplin et al., 2015a in response to van Leeuwen et al., 2015). Here, we respond to Whiten & van de Waal (this volume) by i) discussing how their arguments against our alternative explanations for their conformity interpretation (as advanced in van de Waal et al., 2013) may be misguided, ii) defending the position that their presented correlation between the "majority of individuals" and the "majority of behaviours" is tangential to the current debate, iii) presenting evidence in favour of our original suggestion to keep reliance on the "majority of individuals" and the "majority of behaviours" as two separate learning biases, and iv) realigning the debate between Aplin et al. 2015a and van Leeuwen et al. 2015 to focus again on animals' observation records as prerequisite knowledge to interpret their behavioural decisions in terms of learning biases.

Alternative explanations

In line with Whiten & van de Waal (this volume), we define conformity as "abandoning personal preferences or behaviours to match alternatives exhibited by a majority of others" (Haun, van Leeuwen & Edelson, 2013). In their original study (van de Waal et al., 2013), male vervet monkeys who were trained to prefer one of two food colours in their native group immigrated to a new group where the alternative food colour was preferred and adjusted their preferences accordingly (except for one high-ranking male who maintained his native preference). These immigrants were typically

confronted with a large group of residents feeding from the alternative food colour, while very few or none of the residents fed from the food colour the immigrants were most familiar with (see illustrations in Whiten & van de Waal, this volume). Van de Waal et al. (2013) interpreted these behavioural adjustments by the immigrants as 'conformity'. In response to this interpretation, van Leeuwen & Haun (2014; also see van Leeuwen et al. 2015) pointed out that although the immigrants might have been guided by inclinations to conform to the majority, alternatively, they might have been guided by other (social) learning biases that are independent of majority considerations. For instance, the immigrants might have been focused on copying particular resident individuals, like visibly dominant individuals, or indeed *any* resident individual, precipitated by their immigration-induced stress, anxiety or general state of uncertainty. Whiten & van de Waal (this volume) replied to this suggestion by arguing that any transmission bias other than 'copy-the-majority' is unlikely to explain the switching behaviour of the immigrants. For instance, they argue that the fact that the immigrants do not have female kin in their new group rules out a kin-based learning rule. Likewise, they propose that male vervets are relatively *poor* in recognizing the social hierarchy of females, ruling out a 'copy high-rankers' learning rule (Whiten & van de Waal, this volume). While these particular proposals may or may not be correct, more generally, we wish to emphasize that although field experiments with wild animals are to be applauded for their ecological validity, they do not have any superior claim on epistemological validity. When confounding effects cannot be controlled for rigorously, interpretation of observed patterns need to be made cautiously.

Whiten & van de Waal (this volume) argue most forcefully against the 'random copying' interpretation of their data, stating that: '…for the immigrant vervets to copy just one individual randomly would seem rather *perverse* in the face of the repeated, extensive and quite consistent scenarios of multiple monkey preferences staring

86 immigrants in the face…' (line 95-98). We disagree. Clearly, the sheer availability of
87 information is no guarantee it will be utilized in expected ways, or, at all. Random
88 copying is as good a predictor of the observed patterns of transmission as conformity:
89 When observer monkeys are consistently confronted with the majority of residents
90 feeding from one particular food colour, while only a few, or none, of the resident
91 monkeys feed from the alternative, copying a random individual would,
92 probabilistically, boil down to observer monkeys tending to use the foraging option
93 demonstrated by the majority rather than that demonstrated by the minority, irrespective
94 of observers' particular preference for copying the majority. We consider this a
95 potentially more parsimonious explanation – if observer monkeys could obtain the
96 locally practiced foraging rule by the mere inclination to copy, there is no need for them
97 to apply a cognitively more demanding rule like 'conform to majorities'.
98 Typically, an investigation of whether individuals copy the majority with a
99 higher probability than the relative size of the majority (henceforth 'the disproportionate
100 criterion') is applied to ascertain that individuals are indeed *majority*-biased, or at least
101 to exclude the possibility that individuals merely copy randomly (e.g. Laland, 2004;
102 Mesoudi, 2009). We note that the disproportionate criterion can be viewed as rather
103 stringent and unrealistic for cases in which individuals have already obtained a working
104 strategy, where the key behaviour of interest is the foregoing of prior information for an
105 alternative ('conformity'). Indeed, the disproportionate criterion is typically used in the
106 context of naive individuals setting out to obtain a useful strategy by means of social
107 learning; the context in which *conformist transmission* (CT) is studied (e.g. Boyd &
108 Richerson, 1985; Morgan et al., 2014). In the CT context, when individuals are
109 confronted with a balanced population in which only two possible strategies exist, it is
110 assumed that copiers solely rely on social information and thus have a 50% likelihood
111 of obtaining one or the other strategy. Similarly, when strategy A is wielded by 70% of

112 the demonstrators, and strategy B thus only by 30%, copiers have a 70% likelihood of
113 obtaining strategy A by chance, i.e. if they were to apply a *random copying* rule. To
114 show that individuals *preferentially* copy the majority, and not just by chance, the
115 disproportionate criterion should be adhered to, meaning that in this case copiers should
116 have a likelihood of obtaining strategy A that is significantly larger than 70%. However,
117 in this same example, if individuals are *not* naive and thus have already learned to
118 prefer one strategy over the other, e.g. strategy B, the assumption that they will obtain
119 strategy A or B with a 50% likelihood (in the balanced 2-variant population) is
120 unrealistic. Instead, these experienced individuals will most likely stick to their familiar
121 strategy, in this case strategy B. In a similar vein, experienced strategy B users will not
122 have a 70% chance of ending up with strategy A when 70% of the population they
123 could sample from are strategy A users. If these experienced individuals turn out to start
124 using strategy A with a 70% likelihood, in fact, one could consider this to be a strong
125 indication ('disproportionate' in a sense) of majority influence (see Haun, Rekers &
126 Tomasello, 2014). Thus, contrary to the CT setting, when individuals are experienced, it
127 seems less valid to interpret a copying probability in accord with the relative majority
128 size (here: 70%) in terms of *random copying*: past experience must be weighted in and
129 perhaps a lower threshold than the majority display accepted as strong evidence for
130 conformity (see van Leeuwen & Haun, 2014).
131 For the vervet monkeys (van de Waal et al., 2013), given that i) they were
132 indeed experienced in preferring one food colour over the other when they encountered
133 the opposing demonstrations in the new population, and ii) many of them chose to eat
134 from the food colour in accord with these preference-opposing demonstrations (perhaps
135 in numbers approximately matching the relative majority size, although here, crucially,
136 this cannot be confirmed as the vervets' observation records are missing; see below for
137 more on this topic), this might indicate that 'random copying' could be dismissed as a

mechanistic explanation in favour of 'majority copying'. It is important to note, however, that this conclusion rests on the crucial assumption that no other variables were at play in the decision arena of the respective vervets, which is arguably not true. Notably, the immigrant vervets were leaving behind a familiar home range, and social setting, while moving into an unknown territory with unknown conspecifics ('a different habitat': van de Waal et al., 2013, p. 484). We could envisage the very predicament of the migrating vervets as sufficiently potent to induce a motivation to obtain new, locally more attuned behaviours (ecologically and/or socially). Van de Waal and colleagues (2013; also see Whiten & van de Waal, this volume) acknowledge that such drastic changes in the lives of the vervets could have facilitated the so-called 'copy-when-uncertain' rule (Laland, 2004), a social learning heuristic for which evidence has been found across a wide range of taxa (e.g. see Kendal et al., 2009). They explicitly echo our suggestion by writing: "The fitness of foraging decisions made by wild primates like those we studied will be governed by a host of complex factors that are inherently unknown to foragers, ranging from dietary constituents to plant toxins and competing needs such as predator vigilance: Exploiting the prior discoveries of local experts may be an optimal strategy, overriding opposing knowledge gained in a different habitat such as one's original group." (van de Waal et al., 2013, p. 484). Yet, crucially, neither van de Waal et al. (2013) nor Whiten & van de Waal (this volume) consider the possibility that the 'copy-when-uncertain' heuristic *alone* could have caused the immigrants to adjust their foraging preference upon entering their new environment. It is entirely reasonable that the uncertainty of their new environment changed the default information-gathering mode of the immigrants to "copy" anybody (instead of relying on possibly out-dated and locally inadequate personal strategies).

Given the discussion above, and widespread local foraging traditions, the simplest form of copying – random copying – would equip the immigrating vervets

with the local "majority" strategy. In other words, the transition from home to unknown territory could have reset the vervet monkeys, rendering prior information irrelevant, turning them effectively into naïve learners. We call this the "reset hypothesis". One possible way to empirically test this hypothesis is to investigate whether immigrants would switch to the local foraging preference upon seeing a small number of residents showing a preference against an even larger background of non-behaving others, or, maybe a simpler case, upon seeing just one single resident's demonstration of this preference (something that may have been opportunistically possible to assess had immigrant observation records been acquired, see below). If these observers would switch their preference, *majorities* would cease to be the single possible object of the immigrants' copying efforts. Indeed, drawing on parsimony again, this finding would indicate that "conformity" is not even necessary to explain the immigrants' behaviour. Note that even if one adheres to the conformity definition of 'a willingness to subjugate one's own countervailing knowledge in matching the majority's choice' – as in van de Waal et al. 2013 supplementary material p. 6 – one is still left with the burden of proof for the claim that 'the majority' is being matched, not just any individual.

Overall, the problem with interpreting the observations made by van de Waal et al. (2013) is the lack of nuance in the data regarding observer monkeys responding to different majority/minority ratios of (inadvertent) demonstrator monkeys. If observers are only presented with one stimulus ("the majority"), which consists of many other stimuli ("general social information", "high-ranking individuals", "low-ranking individuals", "conspicuous individuals", etc.), it is impossible to disentangle the very learning bias that the observers follow, while this is exactly what we want to know (e.g. see Heyes, 2016). For instance, if we were to investigate the evolutionary roots of conformist decision-making and we find that immigrant vervet monkeys, patas monkeys and rhesus macaques all adjust their preferences to the majority of the new

group, we would need to know whether they were biased to "the majority" or to any other cue provided by the majority, for without this knowledge, the apparent similarity in decision-making strategies across these species may be purely coincidental.

Majority of individuals versus majority of behaviours

Due to our emphasis (van Leeuwen et al., 2015) upon the need for observation records in interpreting transmission events, we are delighted to find more detailed analysis on the observation records of the vervet monkeys (van de Waal et al., 2013) in their follow-up paper (Whiten & van de Waal (this volume)). Whiten & van de Waal (this volume) present an analysis of how the number of individuals feeding from the locally-preferred food colour correlated with the number of behaviours (handfuls of corn) regarding this same food colour. Specifically, they state: "Indeed the two variables [individuals and behaviours] show a significant correlation across the twelve sample periods ($r = 0.67$, $n = 12$, $p = 0.018$). Accordingly we infer that the migrant males' striking switch from their own to the opposite local preference was an effect of these majority displays, and hence a case of conformity" (Whiten & van de Waal, this volume, L69-73). To clarify, Whiten & van de Waal (this volume) aim to address a subject pertaining to the analysis of *conformist transmission* that was discussed in van Leeuwen et al. (2015) and Aplin et al. (2015a). In summary, where van Leeuwen et al. (2015) argued for keeping separate the biases of following the majority of individuals versus the majority of observed behaviours, and only reserving the term 'conformist transmission' for the former, Aplin et al. (2015a) argued for grouping the biases together under the same term, i.e. 'conformist transmission'. Aplin et al. (2015a) based their argument on the fact that in their original great tit study (Aplin et al. 2015b), the birds did not seem to distinguish between individuals and behaviours (analysed in Aplin et al. 2015a). Following up on this debate, Whiten & van de Waal (this volume) echo Aplin et al.'s position by

showing that in their vervet monkey study (van de Waal et al., 2013) the frequency of *individuals* using a certain behavioural option and the frequency of demonstration of this particular behavioural option in total were not affecting the observers differently. In other words, the monkeys were indistinguishably following the majority of individuals and the majority of behaviours (Whiten & van de Waal, this volume).

While we acknowledge the additional analysis and appreciate its intent, we do not find it compelling for several reasons. First and foremost, in line with our previous arguments, Whiten & van de Waal (this volume) neither use the frequency of individuals nor behaviours to test their conformity hypothesis against any other (social) learning bias. Therefore, the reported correlation between the frequency of individuals and behaviours, while representing an affirmation of internal validity, has no power to falsify alternative hypotheses. For instance, Aplin et al. (2015b), though confronted with similar limitations due to working with wild animal populations, obtained detailed records of birds responding to differently-sized majorities and incorporated their majority numbers, in terms of individuals and behaviours, into statistical analyses to provide insight regarding whether the birds actually *used* the majority cue or merely obtained the most common strategy randomly. Without such analysis, our understanding of transmission biases is not furthered by the reporting of a correlation between two possible measures. Note that due to the very nature of "the majority" (i.e. comprising more than half of the sampled individuals) measures of for instance, skilful, conspicuous and high-ranking individuals will also coincide with the majority strategy.

Furthermore, we note that two cases of correlation between the number of individuals and behaviours indicating the use of a particular strategy (Aplin et al., 2015a and Whiten & van de Waal, this volume) do not constitute sufficient evidence in favour of the two measures being 'functionally equivalent'. While scenarios in which the number of individuals and behaviours correlate are straightforward to envision, we

242 could imagine other scenarios in which the two respective measures would diverge,
243 either due to individual differences in performance rates (in conjunction with relative
244 preferences for certain strategies) or population structure (increasing the likelihood of
245 repetitively sampling the same individuals). Moreover, for reasons of informational
246 accuracy, it may well matter if one individual "cries wolf" ten times, or if ten
247 individuals (independently) do so once (e.g. see Wolf et al., 2013). We conjecture that
248 the adaptive value of relying on indiscriminate sampling of behaviours versus relying
249 on the aggregate knowledge of similarly poised, unpredictability-reducing conspecifics
250 will differ to the extent that under certain conditions, one particular bias is expected to
251 evolve (at the expense of the other). Formal modelling would be a constructive way
252 forward in fuelling our understanding and expectations regarding this pending question,
253 which was acknowledged by Aplin et al. (2015a). In the absence of such understanding,
254 we fail to see how grouping two potentially distinct social learning biases (see Haun et
255 al., 2012) under one and the same denominator of "conformist transmission" could be
256 beneficial to the (comparative) study of learning biases.
257
258 *Methodological concern for using the majority of 'behaviours' instead of 'individuals'*
259 In addition to our conceptual arguments in favour of keeping separate the biases of
260 relying on the majority of individuals versus the majority of behaviours (also see van
261 Leeuwen et al., 2015), we now present a methodological argument in favour of this
262 proposition. Specifically, we note that the gold standard to evidence conformist
263 transmission has been to identify a sigmoidal relation between individuals' probability
264 to copy the majority and the proportional majority size (e.g., see Boyd & Richerson,
265 1985; Chou & Richerson, 1992; Claidiere et al., 2012; Battesti et al., 2015; Aplin et al.,
266 2015b; but see Acerbi et al., under review). A simple agent-based model may help
267 illustrate one of the problems arising from considering the frequencies of *behaviours*,

instead of the frequencies of *individuals*, in detecting this sigmoidal signature of conformist transmission.

Imagine a population of individuals randomly initialised with one of two behaviours, A and B. At each time step, one individual X is randomly selected from the population, and performs its allocated behaviour, and another individual Y is also randomly selected from the population, and then Y always copies the behaviour performed by X. If one plots the relation between the probability of copying a behaviour and the frequency of *individuals* that possess that behaviour at time *t*, the relation is perfectly linear (see Figure 1, left). Each behaviour is, in other words, copied with a probability equal to the frequency of individuals that possess it in the population. This is exactly what we would expect with unbiased – i.e. random – copying (e.g. see Boyd & Richerson, 1985; Henrich & Boyd, 1998; Mesoudi, 2009).

FIGURE 1.

However, if we plot the relation between the probability of copying a behaviour and the frequency of *behaviour* observed in the population, we obtain a sigmoidal relation, that can be mistaken for a signature of conformist transmission (see Figure 1, right). The reason for this result is that, as behaviours where randomly initialised, the total frequency (over all time steps) of the majority behaviour in the population will be, in most cases, lower than the frequency of individuals that possess that behaviour at time *t*. Imagine that behaviour A reaches fixation in the population. The probability to copy A will be 100%, but its cumulative frequency will be somewhat lower, as, at the beginning, at least some individuals performed behaviour B. This behavioural mixture is sufficient to create the effect in the bottom-left and top-right portions of the function, typical of a sigmoidal relation.

294 This effect is an artefact of how populations are initialised in the model, i.e.
295 starting from a random mixture of the two behaviours, but it clearly shows that different
296 analysis may lead to different results. More specifically, in this case, the analysis based
297 on *individuals* reveals perfect linearity, in keeping with the individual-level random
298 copying default, whereas the analysis based on *behaviours* reveals the sigmoidal
299 relation between copying probability and relative frequency characteristic of conformist
300 transmission (see Aplin et al., 2015b). In other words, the analysis based on *behaviours*
301 leads to a detection of conformist transmission where clearly there is none (because all
302 copying here is *random*).
303 A slightly more complex model shows an analogous result, without the need to
304 initialise the populations in the above way. In this set-up, populations start naïve, and
305 the two possible behaviours are instead introduced through individual innovations (each
306 behaviour – A or B – with the same probability). Note that this set-up reflects the
307 scenario in which conformist transmission is typically studied (e.g. Boyd & Richerson,
308 1985; Henrich & Boyd, 1998; Morgan & Laland, 2012; van Leeuwen & Haun, 2014).
309 The guiding copying mechanism is exactly the same as in the previous model, i.e.
310 random copying remains the only form of copying. The only twist in our new model is
311 that innovation rate decreases over time, mimicking individuals gradually converging
312 on a certain variant preference (we believe this to be a realistic scenario). The results are
313 analogous to the previous model: an analysis based on *individuals* shows perfect
314 linearity in keeping with the random copying default, but an analysis based on
315 *behaviours* reveals a sigmoidal relation between copying probability and the variant
316 frequency in the population (see Figure 2). The reason for this result is that an initial
317 innovation rate creates a situation in which both behaviours become present – similar to
318 the random mixture of behaviours with which the populations were initialised in the
319 first model – and, after that, populations again converge on one of the two behaviours,

as innovation becomes less influential. Regardless, it is striking that even in the more typically studied scenario of naive individuals exploring a novel cultural landscape (the conformist transmission scenario), the illusion of conformist transmission can still emerge when analysis focuses on *behaviours* instead of *individuals*.

FIGURE 2.

In conclusion, for reasons of conceptual, empirical and methodological clarity, we propose to keep the study of conformity and conformist transmission restricted to the level of *individuals* and pursue the study of the effects of repetitive exposure to stimuli or behaviours, regardless of their executors, in its own right. Accordingly, we note that in the seminal conformity studies "the majority" did not consist of *behaviours* but *individuals*. For instance, in the Asch studies (1956), "the majority" was assembled by a group of confederates each expressing one opinion, not by one confederate expressing his/her opinion multiple times (for studies on the (mere) exposure effect, see e.g. Bornstein, 1989; Zajonc, 1968).

The pivotal role of observation records

Finally, we wish to draw attention to the most prominent matter highlighted by van Leeuwen and colleagues (2015) in reference to the study of conformity in particular and social learning biases in general: observation records. Underlying all previous considerations, e.g. whether or not the social learning rule 'copy high-rankers' could explain the patterns described in van de Waal et al. (2013), lies the implicit assumption that the respective decision-makers have observed all available social information. We challenge this assumption and wish to emphasize that when it comes down to pinpointing (social) learning biases, it is essential that observation records are obtained

346 and used in analysis, especially given that such data are accessible (e.g. see van
347 Leeuwen et al., 2013; Kendal et al., 2015).
348 Whiten & van de Waal (this volume) respond to our previous criticism that in
349 their original study (van de Waal et al., 2013) it was 'unknown what and whom the
350 immigrating males had observed prior to their preference switching' (van Leeuwen et
351 al., 2015, p.3) by stating that this is true for all studies, including experimental ones like
352 that conducted by Haun and colleagues (2012). However, our criticism did not refer to
353 the actual observations made by individuals – we agree that a certain level of
354 assumption, ultimately even when using eye-tracking or more advanced technologies, is
355 unavoidable. Instead, our criticism pertained to the assumption that the immigrants were
356 somehow able to obtain knowledge of the available social information. The immigrant
357 vervets' observation records were entirely absent in the original study claiming to have
358 identified conformity (van de Waal et al., 2013) and remain too imprecise for the
359 investigation of conformity in the follow-up analysis (Whiten & van de Waal, this
360 volume). In the first instance, we refer to records of what/whom the vervets could have
361 observed because they were *present* when the social information (which would need to
362 be quantified per observation bout) was available. In the second instance, head
363 orientation during the inadvertent demonstrations seems a crucial measure to report.
364 Such measures provide the necessary information to link an individual's observational
365 input (in this case: social information) to an individual's behavioural output (in this
366 case: maintaining or adjusting food colour preference), and thus the relevant
367 information to draw conclusions on individuals' specific learning biases.
368 Another example of individuals' observation records receiving insufficient
369 consideration concerns the recent great tit study by Aplin and colleagues (2015b). While
370 this study provides detailed analyses of the birds' tendencies to learn socially,

including, importantly, their propensities to copy in response to different majority sizes, the very data central to their conformist transmission analyses rest on assumptions rather than observations. The authors derived an external measure of which birds typically flocked together and calculated an average 'group length' of flocking (i.e. 245 seconds) that was subsequently used during the experiment in order to *assume* that all birds operating the experimental task in this time-window obtained knowledge of each other's choices. In other words, the authors did not score which birds were simultaneously present at the experimental task (or which birds observed each other), but instead relied on the assumption that the birds were in the vicinity of the experimental task at the same time as the birds that were considered to be "demonstrators", and the further assumption that they paid attention to those demonstrations (see Aplin et al., 2015b). We feel this to be an unfortunate caveat in an otherwise excellently conceived and conducted study. Regardless of the plausibility of such assumptions, observational input is the very measure from which we aim to derive conclusions on individual's (social) learning biases, which, in our view, makes it imperative to be as accurate as possible. We wonder, for instance, whether the birds with the most extreme copying probabilities (0 and 100%) had observed that the entire sub-group of their sub-population had not converged on one particular strategy (see Figure 1 in Aplin et al., 2015a). These data seem crucial for the sigmoidal pattern to emerge, which was used to argue for conformist transmission in the birds' social learning patterns (Aplin et al., 2015b). Notably, new modelling insights show that this very sigmoidal pattern can emerge in the absence of individuals' being conformist biased (Acerbi et al., under review), making it even more pertinent to know what the birds observed exactly.

References

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015a). Counting conformity: evaluating the units of information in frequency-dependent social learning. *Animal Behaviour, 110,* e5-e8. doi:10.1016/j.anbehav.2015.09.015

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015b). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature, 518,* 538-541. doi:10.1038/nature13998

Asch, S. E. (1956). Studies of Independence and Conformity .1. A Minority of One against a Unanimous Majority. *Psychological Monographs, 70*(9), 1-70.

Battesti, M., Moreno, C., Joly, D. & Mery, F. (2014). Biased social transmission in Drosophila oviposition choice. *Behavioral Ecology and Sociobiology, 69,* 83–87.

Bornstein, R. F. (1989). Exposure and affect: Overview and meta-analysis of research, 1968-1987. *Psychological Bulletin, 106,* 265-289.

Boyd, R., & Richerson, P. (1985). *Culture and the Evolutionary Process*. Chicago: University of Chicago press.

Chou, L. S. & Richerson, P. J. (1992). Multiple Models in Social Transmission of Food Selection by Norway Rats, Rattus-Norvegicus. *Animal Behaviour, 44*(2), 337-343.

Claidière, N., Bowler, M. & Whiten, A. (2012). Evidence for weak or linear conformity but not for hyper-conformity in an everyday social learning context. *PLoS One, 7,* e30970.

Hastie, R., & Kameda, T. (2005). The robust beauty of majority rules in group decisions. *Psychological Review, 112*(2), 494-508. doi:10.1037/0033-295x.112.2.494

Haun, D. B. M., Rekers, Y., & Tomasello, M. (2012). Majority-biased transmission in chimpanzees and human children, but not orangutans. *Current Biology, 22,* 727-731. doi:10.1016/j.cub.2012.03.006

Haun, D. B. M., Rekers, Y., & Tomasello, M. (2014) Children conform to the behavior of peers; other great apes stick with what they know. *Psychological Science, 25*, 2160 - 2167. doi:10.1177/0956797614553235.

Haun, D. B. M., van Leeuwen, E. J. C., & Edelson, M. G. (2013). Majority influence in children and other animals. *Developmental Cognitive Neuroscience, 3,* 61–71.

Henrich, J., & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior, 19*(4), 215-241.

Heyes, C. (2016). Blackboxing: social learning strategies and cultural evolution. *Philosophical Transactions of the Royal Society B-Biological Sciences, 371*, 20150369.

Kendal, R. L., Coolen, I., & Laland, K. N. (2009). Adaptive trade-offs in the use of social and personal information. In R. Dukas & R. J. (Eds.), *Cognitive ecology II.* (pp. 249-271). Chicago: University of Chicago Press.

Kendal, R. L., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and Human Behavior, 36,* 65-72.

Laland, K. N. (2004). Social learning strategies. *Learning & Behavior, 32*(1), 4-14.

Mesoudi, A. (2009). How Cultural Evolutionary Theory Can Inform Social Psychology and Vice Versa. *Psychological Review, 116*(4), 929-952. doi:10.1037/0017062

Morgan, T. J. H., & Laland, K. N. (2012). The biological bases of conformity. *Frontiers in Neuroscience, 6*(87). doi:10.3389/fnins.2012.00087

Morgan, T. J. H., Laland, K. N. & Harris, P. L. (2014). The development of adaptive conformity in young children: effects of uncertainty and consensus. *Developmental Science, 18*(4), 511–524.

Tennie, C., Fischer, J., Haun D. B. M., & Galef, B. G. (2013). Conformity in wild vervet monkeys? Possibly not. *Online comment* on "Potent social learning and conformity shape a wild primate's foraging decisions" by van de Waal et al. 2013. http://comments.sciencemag.org/content/10.1126/science.1232769

van Leeuwen, E. J. C., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. M. (2013). Chimpanzees flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *Plos One, 8*(11). doi:10.1371/journal.pone.0080945

van Leeuwen, E. J. C., & Haun, D. B. M. (2013). Conformity in primates: fad or fact? *Evolution and Human Behavior, 34*, 1-7.

van Leeuwen, E. J. C., & Haun, D. B. M. (2014). Conformity without majority? The case for demarcating social from majority influences. *Animal Behaviour, 96*, 187-194.

van Leeuwen, E. J. C., Kendal, R. L., Tennie, C. & Haun, D. B. M. (2015) Conformity and its look-a-likes. *Animal Behaviour, 110,* e1-e4. doi:10.1016/j.anbehav.2015.07.030

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent Social Learning and Conformity Shape a Wild Primate's Foraging Decisions. *Science, 340,* 483-485. doi: 10.1126/science.1232769

Whiten, A. & van de Waal, E. (2016). Animal Behaviour. THIS VOLUME.

Wolf, M., Kurvers, R. H. J. M., Ward, A. J. W., Krause, S., & Krause, J. (2013). Accurate decisions in an uncertain world: collective cognition increases true positives while decreasing false positives. *Proceedings of the Royal Society B-Biological Sciences, 280*. doi: 10.1098/rspb.2012.2777

Zajonc, R. B. (1968). Attitudinal effects of mere exposure. *Journal of Personality and Social Psychology Monographs, 9*, 1-27.

Figure Legends

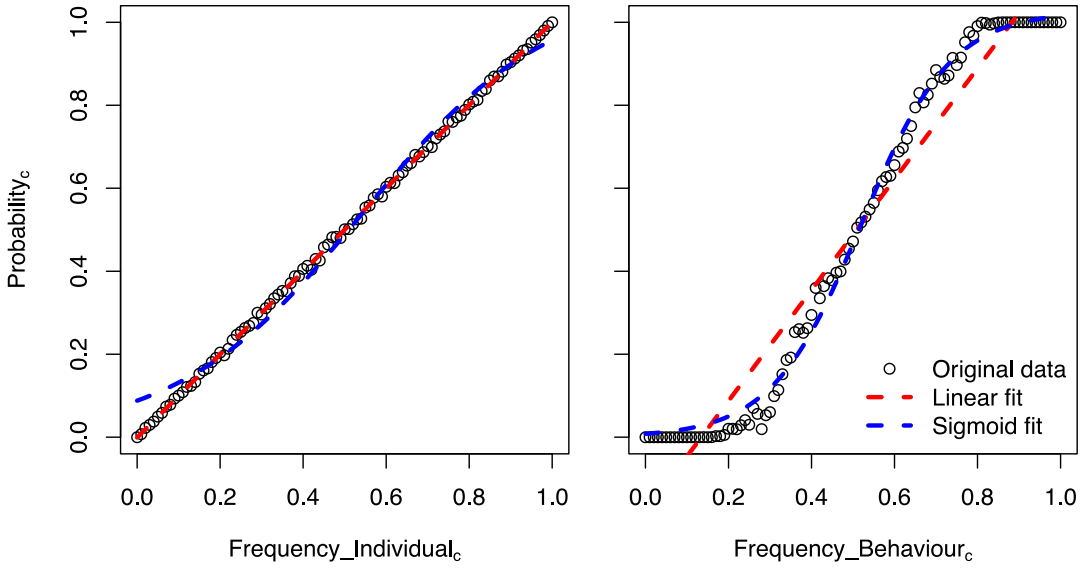
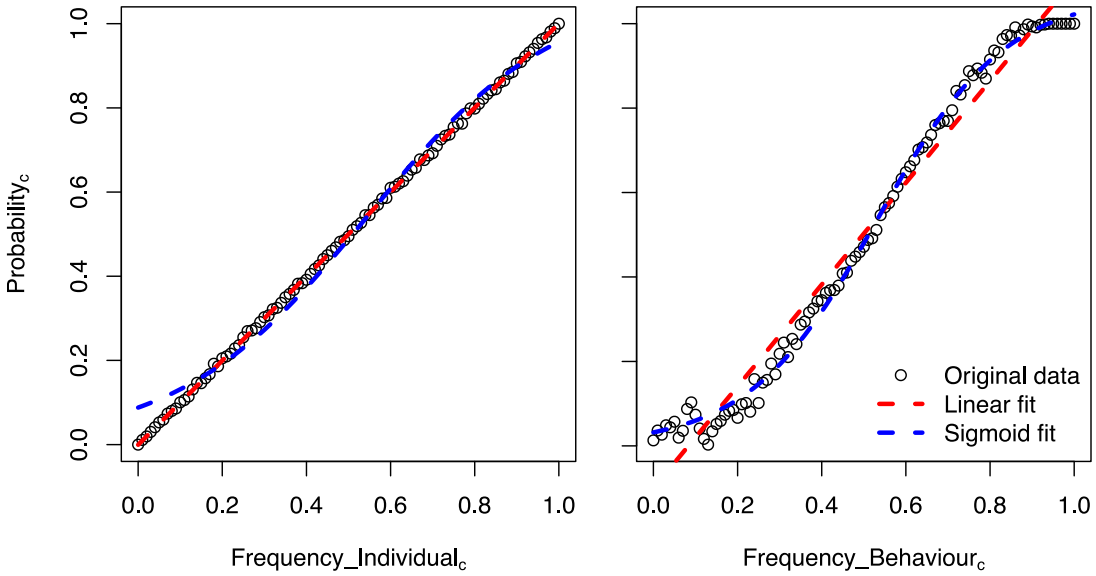


Figure 1. A population of N=100 individuals is randomly initialised with one of two behaviours. At each time step, a model and an observer are randomly extracted from the population, and the observer always copies the model. The simulation ends at 10,000 time steps, i.e. 10,000 possible interactions. Results are based on 1,000 replications of the model. Simulated data are fitted with a linear and a sigmoid model. Copying probability is plotted against frequency of individuals (a), and frequency of behaviours (b).



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489 **Figure 2.** Simulations start with a population of N=100 naïve individuals. At each time
490 step there is a probability that an individual, randomly extracted from the population,
491 will innovate, i.e. will introduce, with equal probability, one of the two possible
492 behaviours. Probability of innovation is initially equal to μ=.1 (one innovation every 10
493 time steps on average), and decreases exponentially with time, according to $e^{-5t/T}$,
494 where *t* is the current time step, and *T* is the maximum amount of time steps. In
495 addition, at each time step, a model and an observer are randomly extracted from the
496 population, and the observer always copies the model. The simulation ends at 10,000
497 time steps, i.e. 10,000 possible interactions. Results are based on 1,000 replications of
498 the model. Simulated data are fitted with a linear and a sigmoid model. Copying
499 probability is plotted against frequency of individuals (a), and frequency of behaviours
500 (b).